Evolutionary dynamics of the elevational diversity gradient in passerine birds

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ABSTRACT

Low elevation regions harbor the majority of the world's species diversity compared to high elevation areas. This global gradient suggests that lowland species have had more time to diversify, or that net diversification rates have been higher in the lowlands. However, highlands seem to be cradles of diversity as they contain many young endemics, suggesting that their rates of speciation are exceptionally fast. Here, we use a phylogenetic diversification model that accounts for the dispersal of species between different elevations to examine the evolutionary dynamics of the elevational diversity gradient in passerine birds, a group that has radiated globally to occupy almost all elevations and latitudes. We find strong support for a model where passerines diversify at the same rate in the highlands and the lowlands but where the per capita rate of dispersal from high to low elevations is more than twice as fast as in the reverse direction. This suggests that while there is no consistent trend in diversification across elevations, part of the diversity generated by highland regions migrates into the lowlands, thus setting up the observed gradient in passerine diversity. We find that this process drives tropical regions but for temperate areas, the analysis could be hampered by their lower richness. Despite their lower diversity, highland regions are disproportionally important for maintaining diversity in the adjacent lowlands

Keywords: lineage dispersal; diversification rates; species elevation distributions; species pump

The striking differences in the form and diversity of life as one travels up mountains is one of the most prominent and long recognized patterns in biogeography [1]. Across animals and plants, and across mountains globally, diversity tends to peak at low or intermediate elevations and then declines towards mountain summits [2,3]. Thus, while mountain regions are global hotspots of diversity [4,5], most species occur in the lowlands with relatively few species in the highlands. One possible explanation for this global elevational diversity gradient (EDG) is that for most organism groups, there has been more time for species to accumulate at low to intermediate elevations, with highland environments only colonized more recently [6]. Another, but not mutually exclusive, possibility is that net rates of diversification are faster in the lowlands, because the greater area or energy availability increases the ecological limit to diversity or promotes faster intrinsic rates of speciation and lower extinction [7]. Yet, there is also evidence that highland regions may be cradles of species diversity, characterized by exceptionally fast rates of speciation [8,9]. In other words, speciation may be fastest at high elevations, even though species diversity is currently lowest there [3]. This suggests a third possible factor contributing to the EDG: species generated in disproportionally larger numbers in the highlands migrate to the lowlands.

Macroecological studies of current species distribution patterns have long supported the idea that highlands may be hotbeds of evolution, especially in the tropics [10]. Large numbers of endemic species are concentrated on tropical mountains, far more than would be expected by chance or current climate [11]. More recent phylogenetic studies have shown that many of these endemic species are comparatively young, pointing towards rapid speciation [12,13]. There are various reasons why rates of speciation may be faster at high elevations, including the fragmentation of habitats on different mountain summits [13], ecological opportunity as new habitats were made available during recent mountain uplift [14], exposure to higher levels of ultraviolet radiation boosting rates of mutation [15], and the susceptibility of species inhabiting narrow thermal bands to become isolated by the expansion of glaciers during recurring ice ages [12,16]. All these factors are thought to be particularly important in the tropics because limited seasonal variation enables the greater thermal stratification of species across mountain slopes, enhancing opportunities for geographic isolation and divergent ecological selection [17]. However, while some studies have supported the idea that diversification is faster in the highlands [18], others studies have found no evidence for differences in diversification rates across elevations [19], and thus whether rates of diversification vary consistently across elevation remains debated.

One explanation for this lack of resolution is that the dynamics of the EDG may be highly variable, differing between mountain regions with contrasting geological histories and geographic properties [20]. For instance, some highland lineages in the Andes have undergone explosive radiations, but such cases appear to be less common in mountain systems in the Afrotropics [20]. In addition, gradients in diversity — as well the phylogenetic branching times used to model these gradients — arise not only from differences in diversification but also the dispersal of lineages across elevations. Yet, models accounting for both differences in diversification as well as the movement of species between elevational bands have rarely been applied. Some verbal models predict that highland communities are evolutionary sinks, derived primarily from the lowland taxa either invading or being passively transported to higher elevations during mountain uplift [21]. Other verbal models predict that highland regions act as species pumps, with lineages arising at higher elevations moving downslope [21–25], providing an important contributor to the greater diversity of the adjacent lowlands, and leading to high species richness at the ecotone between mountains and lowlands, particularly in the tropics[2,3]. Given this complexity, establishing the evolutionary dynamics of the EDG requires developing empirically testable models that integrate the processes of diversification and dispersal while also accounting for potential differences in diversification dynamics across species, latitudes and regions.

Here, we study the dynamics of the EDG of passerine birds, a global ‘super radiation’ of exceptional diversity, including approximately 5700 species, found at almost all elevations, latitudes and biogeographic realms (other than Antarctica). Passerines have arisen in approximately the last 47 million years [26], and represent an ideal study group. Passerines show a clear EDG, with over 8 times as many species present in the lowlands (n = 5095, lower elevation bound < 1500 m) as there are mid (> 1500 m) or high (> 3000 m) elevation specialists combined (n = 611) (**Figure 1**; **Supplementary Table 1**). The sheer diversity of passerines, combined with the availability of phylogenetic trees [27], provides substantial power for comparing competing scenarios of diversification and dispersal between different elevation bands (**Figure 1**). Importantly, although characterizing the distribution of species in topographically diverse regions is challenging, the elevational ranges of passerines are relatively well known, with estimates of upper and lower elevation limits available for almost all (96%) species.

Using this dataset, we first examine the relationship across passerines between the elevational state of a species and its tip-DR metric, which reflects speciation rate [28] and has previously been applied to test for latitudinal and elevation gradients in avian evolutionary rates [3]. Because this metric does not account for the movement of species between elevational bands, we then apply a recently developed dynamic phylogenetic model (SecSSE, [29]), that in addition to testing for elevation-dependent rates of speciation and extinction, also enables us to account for the transition of species between different elevational states over evolutionary time. Using this dynamic model, we are also able to test whether species movement downhill is faster or slower than the rate of movement uphill, and thus whether highlands act a source or sink of species diversity respectively. Finally, because there is evidence that rates of diversification in passerines may vary between the tropics and temperate zone [30] and between the New and Old World [27] we allow rates of speciation (or extinction) to vary either between different longitudinal (Old and New World) or latitudinal (tropics and temperate) regions, when testing for an effect of elevation (**Figure 2**).

RESULTS

Diversification and dispersal across elevations

When comparing the tip-DR of species currently occurring in the lowlands and the highlands, rates of speciation are inferred to be slightly but significantly faster in the highlands. This is consistent with previous assemblage-level analyses, indicating that the average tip-DR of highland bird assemblages is greater than that of lowland bird assemblages [3]. However, closely related species show a strong tendency to share similar tip-DR values (Pagel's $\lambda = 0.987$, 95% CI: 0.984-0.99), and thus any association between elevation and speciation rate could be driven by phylogenetic non-independence. In accordance with this, when shared ancestry is accounted for with a phylogenetic generalized linear model (PGLS), the relationship between elevation and tip-DR disappears (**Supplementary Table 2**).

While this result suggests that there is no association between elevation and speciate rate, this analysis must be interpreted with caution because it assumes that species distributions are static and thus does not account for the movement of species between different elevational bands over evolutionary time. To address this shortcoming, we next fitted a dynamic model that estimates the diversification rate associated with each elevation state as well as the transition rates between these states. We compared the fit of a model in which rates of speciation (or extinction) vary across elevation to two alternative null models. First, a constant rate model, in which all lineages share an identical rate of diversification. Second, a concealed-trait dependent model, in which rates of diversification are allowed to vary across lineages due to another 'hidden' trait, but they do so independently of elevation. This second null model is more realistic because it accounts for the possibility that rates of diversification have been heterogeneous across passerines, and means that support for elevation-dependent rates of diversification does not arise simply because of the unrealistic assumption of a constant rate of diversification across such a large clade.

When compared to a standard constant rate (CR) null model, in which rates of diversification are equal across elevational states, an Elevation-dependent (ED) model, in which rates of diversification increase with elevation, is more strongly supported. This result seemingly supports previous analyses suggesting faster rates of bird diversification in the highlands [3]. However, when compared to a concealed trait-dependent (CTD) null model, in which rates of diversification are allowed to vary across lineages but independently of elevation, the CTD null model is overwhelmingly supported (AICw ~ 0.99). Thus, while our results provide substantial support for a scenario in which diversification rates vary across lineages, this variation is likely due to other factors than elevation (**Supplementary Table 3)**. The best supported model is a latitudinal-CTD model, in which rates of speciation are 1.4 times faster in the tropics than the temperate zone. Across all models, extinction is estimated to be low (latitudinal-CTD model, μ = 0.0001/myr) and a latitudinal-CTD model with heterogeneity in rates of speciation, is more strongly supported than a CTD model with heterogeneity in rates of extinction across lineages and/or regions. Finally, we find no evidence for differences in rates of diversification between the Old and New World (**Supplementary Table 3)**.

While we find no effect of elevation on rates of diversification, we find substantial differences in rates of downhill and uphill dispersal**.** According to the best model, the estimated per lineage rate of downhill dispersal is 0.189/myr, substantially faster than the uphill dispersal rate of 0.072/myr (**Figure 2**). This model of faster downhill dispersal is much more strongly supported than an alternative expansion-contraction scenario, in which rates of elevational range expansion and contraction may differ, but there is no difference between uphill and downhill movement (**Figure 2**). The best-supported model allows transition rates between elevational states to differ from those of the transition rates between the concealed trait states, rather than assuming that these are identical (**Supplementary Table 3**), even though the former model has more parameters**.** We find, as may be expected, that lineages disperse between continents at rates that are smaller than dispersal across elevational bands. The best model shows that the rate of lineage exchange between the tropics and temperate zone is 0.0187/myr with lineage dispersal between the Old Word and New World occurring at a rate of 0.00016/myr (**Figure 2**). Note that all these rates are per-lineage rates.

Most passerines are tropical and so to test whether our results hold when using a tropical subgroup, we repeated our analysis focusing on the ovenbirds, a large tropical radiation (*n* = 285 species). Ovenbirds are spread across latitudinal bands in similar proportion as the entire dataset, they inhabit only the New World tropical region, and a high quality and comprehensively sampled phylogenetic tree is available[31]. The results for ovenbirds are consistent with those from the global analysis, with no evidence of differences in diversification across elevation, and the Uphill-Downhill model receiving the highest support, with the rate of downhill dispersal (0.3176) substantially exceeding the rate of uphill dispersal (0.1538).

Species whose modern distribution suggests limited access to mountain ranges first have to expand their range in the lowlands before being able to move to a higher elevation. To test whether these species influence the inferred differences in rates of uphill and downhill dispersal, we added an additional state (L-) to our model. The L- was assigned to lineages without direct access to mid- and high-montane areas anywhere in their range or abutting their range (i.e., either island endemics or species with a localized lowland distribution; n = 146). Even after accounting for these species, our conclusions remained unchanged (**Supplementary Table 4)**, with no evidence for differential diversification across elevation but strong support for faster downhill that uphill dispersal.

Geographic origin of passerines and accumulation of lineages over time

Because the elevational origin of passerines can have an important influence on the current gradient of species richness, we extracted the probabilities (using the best supported model) of each state (i.e., the combination of elevation and latitude) at the most-basal node of the phylogeny to estimate where the clade first appeared. These probabilities indicate the most likely state of the ancestral species just before it splits at the crown of the phylogeny, and so the true origin of the clade (at the stem age) may have been different. Regardless of whether rates of diversification are allowed to vary with latitude or longitudinal region, a highland origin of passerines is equally well supported as a lowland origin. This lack of strong support for either elevational state reflects the relatively rapid transitions across elevation inferred by our analysis and which have likely erased this historical signal of where passerines originated.

DISCUSSION

In spite of clear differences in passerine diversity at different elevations, we find no difference in diversification rates across elevational zones. Instead, the best supported scenario is a Latitudinal-Concealed-Trait Dependent model with higher per capita rates of downhill dispersal than uphill dispersal. This CTD model indicates that there is substantial variation in diversification rates across lineages and latitude, but that this variation is not related to elevation. Thus, while previous more taxonomically or geographically focused studies have found evidence for differences in diversification across elevation, this is not supported by our global analysis across all passerines.

The absence of a consistent effect of elevation on diversification is unlikely to be explained by a lack of statistical power. Our analysis contains thousands of species and our model did detect faster rates of diversification in the tropics compared to the temperate zone. This suggests that if there was a globally coherent effect of elevation on diversification, this would also have been detected in our analysis. Furthermore, the absence of any effect of elevation on diversification cannot be explained by a failure of our model to detect finer-scale heterogeneity in diversification rates within the tropics or temperate zone. The strong support for the Concealed Trait-Dependent model confirms that there is indeed substantial heterogeneity in rates of diversification across passerines within these regions, but that this variation is not aligned with elevation. Critically, our results show that failure to account for this background heterogeneity in rates of diversification would have led to the spurious conclusion that rates of diversification do increase with elevation. We therefore suggest that application of such a Concealed Trait-Dependent model is an important advance that should also be applied when examining other putative drivers of diversification rates (e.g., body size).

One possible explanation for why our global analysis does not detect an elevational gradient in diversification, is that different dynamics may prevail in different regions obscuring the overall importance of elevation. Differences across latitude may be particularly important in this regard, because it is mainly highlands in the tropics where rates of speciation are thought to be promoted [32]. However, this is unlikely to explain our results because most of the species in our analysis (85%) occur in the tropics, and thus it is the dynamics of the EDG in this region which dominate our model inferences. Indeed, our results based on the tropical ovenbirds are highly consistent with the general pattern. Rather, our results suggest that net rates of diversification are boosted in the tropics, but this occurs regardless of elevation.

Another possibility is that although diversification and elevation may be related in some mountain systems, these effects of elevation are highly context dependent, determined by the particular geological history and environment in different mountains [3]. Accounting for such variability is challenging because it would require a substantial increase in model complexity and the number of parameters that need to be inferred. We note that support for such a complex model would not alter our main conclusion that, at a global scale, there is no consistent trend in diversification across elevation.

Our finding that net rates of diversification in passerines do not vary consistently with elevation contrasts with that of a recent study showing that diversification rates increase with elevation [3]. We note a number of important methodological differences that may explain these contrasting findings. Quintero and Jetz (2018) calculated speciation rate for each extant passerine species (tip-DR) and then averaged this across all the species inhabiting each elevational band across major mountain systems. This approach strongly differs from ours, because it mainly captures recent speciation and because it links the speciation rate of a lineage to its current elevation. This approach ignores dispersal across elevational bands and thus the possibility that the speciation events leading to a particular lineage occurred at a different elevation to where that species currently resides. Furthermore, while the shared phylogenetic history of each species is automatically accommodated in our dynamic model (i.e., each branch of the tree is only counted once), our results show that treating each species as statistically independent when analyzing tip-DR may lead to spurious results. On the basis of these results, we suggest that accounting for the biogeographic dynamics and phylogenetic non-independence of lineages is likely to be critical when making inferences of how rates of diversification vary across elevation or any other gradient.

Much of the research on the evolutionary dynamics of the EDG has focused on explaining patterns at relatively fine taxonomic scales or particular mountain systems. While these have provided evidence for both uphill [33] and downhill [34] movement of species, they have often supported the idea that most clades originated in the lowlands and then invaded higher elevations [35]. For example among avian genera, *Leptopogon* flycatchers [23], Chat-tyrants [25], *Andropadus* greenbuls [24] and *Thamnophilus* antshrikes [36] show a repeated movement of species into the highlands followed by in situ diversification. Larger and older clades, however, paint a more complex picture, with McGuire et al (2007) providing evidence that hummingbirds (Trochilidae) have undergone multiple colonizations of Andes from the lowlands, but also the reverse.

Our findings across passerines, place these previous genus- and family-level studies in a broader context, showing that while there are many cases of uphill dispersal followed by radiation, overall, on a per-lineage basis, the dispersal from high to low elevations, occurs at a much faster rate.

Why per-lineage rates of dispersal from highlands to lowlands are faster than the reverse remains unclear. Indeed, most studies have suggested a net movement of species uphill, either because of ecological opportunity [14] or passive transportation during mountain uplift [21]. A non-biological explanation of higher rates of dispersal downhill than uphill could be that available area decreases with elevation, which allows more species to fit in the lowlands. Another possible mechanism is that strong physiological limitations prevent adaptation to higher elevations (i.e., UV-radiation and oxygen availability vary across altitude). For instance, bird species living at high altitude show a loss of genes related to immune response and require a specific machinery to repair cellular damage caused by UV radiation [37]. Lineages adapting to highlands and losing immune function might be unlikely to regain it. However, the return to lowlands or the adaptation to lowlands by highland-originated lineages could be mediated by the stronger expression of immune response boosted by high levels of oxygen [38]. Additionally, decreased oxygen concentration can severely increase the chances of hypoxia during flight [39]. Although phenotypic plasticity could partially tackle this limitation [40], evolutionary adaptations involving changes in hemoglobin affinity to oxygen may be difficult to develop as there are few molecular pathways that are not associated with reduced fitness i.e., deleterious pleiotropic effects [41]. Furthermore, species adapted to low concentration of oxygen require large lungs that are costly to maintain so the switch to a lowland region might be beneficial from an energetic standpoint [42]. It is important to note that we are reporting the rates of successful dispersal events between elevational bands and that dispersal events not leading to establishment are not recorded. Hence, another alternative is that high elevation habitats may be less conducive to colonization over macro-evolutionary timescales [43] due to ecological constrains i.e., a lower availability of resources [7]. In other words, it is possible that lineages are equally likely to disperse regardless of the elevation they arise from, but those elevational bands where the niche space is wider, are more likely to accommodate colonizers. Thus, our results are potentially consistent with the idea that higher ecological limits to coexistence in the lowlands ultimately underlie the EDG in passerine birds [44].

Our results provide support that highland regions have acted as a species pump for passerine birds, not because of faster total rates of diversification, but because species arising in the highlands disperse downhill. Thus while highlands constitute only a fraction of passerine diversity they play a disproportionate role in boosting the diversity of the lowlands. Highland species are at particular risk of extinction from anthropogenic warming this century due to a lack of available cooler habitats to which species can disperse [45]. Our results suggest that the loss of highland lineages will also have long term impacts on the diversity of the lowlands and passerines globally.

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Author Contributions

PvE collected data; LH-A and PvE performed the analysis; RSE and ALP supervised the project; LH-A, PvE, ALP and RSE wrote the manuscript.

Competing Interests statement

The authors declare no competing interest.

FIGURES

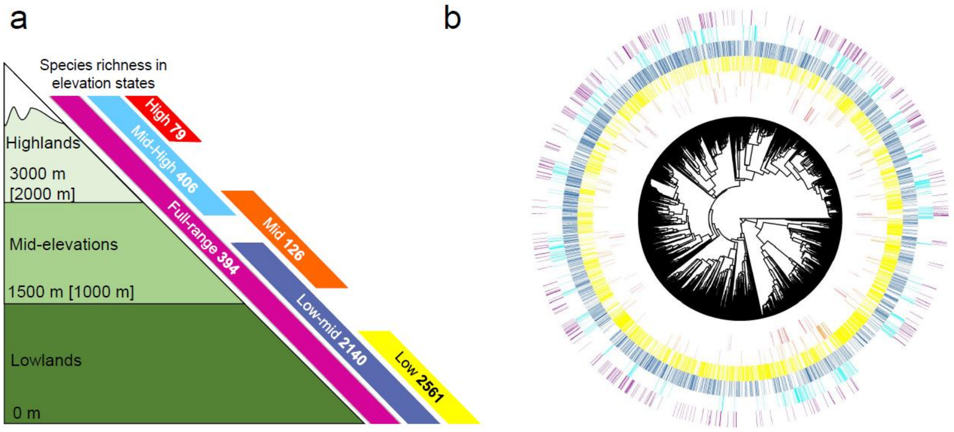

Figure 1. The global elevational diversity gradient (EDG) in passerine birds. a) species richness in birds exhibits a decline with elevation. The three assigned elevational bands (altitudinal delimitation for temperate regions is in brackets) and six possible elevational states of species are shown, with the number of species in each state indicated. States account for species restricted to a single elevational band or that span multiple elevational bands. b) the distribution of species across elevational bands within the passerine phylogenetic tree, with elevation states plotted concentrically onto the phylogeny. Colors match those in 1a.

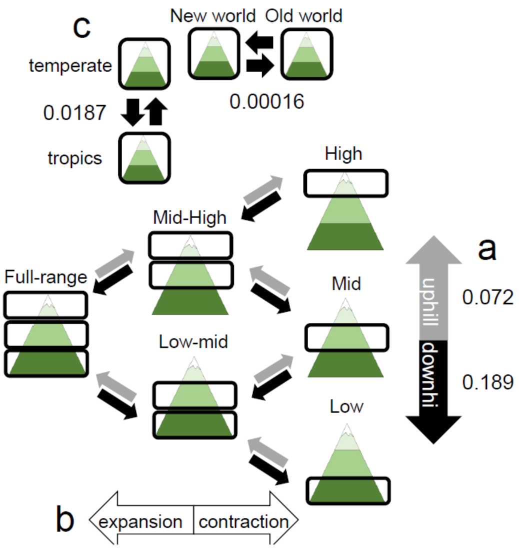

Figure 2. The dynamics of the EDG is modelled by allowing rates of diversification to vary across species elevational states and by allowing transitions between different elevational states over time. We model transitions between states by considering that species contract their elevational range when they become absent from an elevational band and expand their elevational range when they become present in a new elevational band. We consider two possible scenarios of how species transition between elevational states. First, in the uphill-downhill scenario (a), the rate of transition to a higher elevational state can differ from rate of transition to a lower elevational state. Second, in the expansion-contraction scenario (b), the transition to a wider elevational state (i.e. present in more elevational bands) can differ from the rate of transition to a narrower elevational state (i.e. present in fewer elevational bands). In addition to transitions between elevational states, species may also transition between either different biogeographic states, indicated either by their presence in the old or new world or the temperate or tropical zone (c). We show the per-lineage rates of transition across longitude, latitude and elevation which maximize the likelihood of the best supported model.

METHODS

Phylogenetic framework

We used a Bayesian pseudo-posterior distribution of time-calibrated phylogenies [27], which includes 9,993 of 10,473 currently recognized bird species. Using the program TreeAnnotator from the BEAST2 package v2.4.2 [46] we produced a maximum-clade credibility tree from all available stage 2 trees with the Hackett backbone. We pruned this tree to the level of Passeriformes (n = 5,966 species). We are aware of the shortcomings of using a megaphylogeny that does not include sequence data for each taxon [47], but the statistical power achieved by the large number of tips and branching events compensates, at least in part, for the possible lack of taxonomic precision. To test if our results hold in a subset, we repeated out analysis using a phylogeny for ovenbirds (Furnariidae) for which 97% of species have been sequenced [31].

Elevation data and large-scale realms

We compiled elevation data for passerines, recording lower and upper elevation bounds of their distribution, based on descriptions in the Handbook of the Birds of the World [48]. We did not include occasional records at extreme elevation. Elevational distributions are based on the breeding range, thus excluding wintering and transient elevation records. Species without known elevational distribution were assigned NA in the data set (n = 260) rather than removed, because this could bias diversification rates, and our analysis can account for this missing data (see below).

Our model of elevation-dependent diversification and dispersal requires treating elevation as a categorical state. To do this we defined 3 elevational bands whose altitudinal range vary latitudinally. In tropical regions: lowlands (from sea level up to 1500 meter above sea level), mid-elevations (1500 - 3000 m), and highlands (> 3000 m). In temperate regions: lowlands (from 0 to 1000 m), mid-elevations (1000 - 2000 m), and highlands (> 2000 m). These categories broadly agree with those established by [49] for Neotropical montane birds based on the dominant vegetation associated with the tropics, subtropics, and alpine zones, respectively. Species may inhabit multiple bands (indeed some species span the entire elevation gradient) and accounting for this variation in elevational range size is important when determining the dynamics of the EDG. We therefore defined three additional categories for species inhabiting more than one elevational band: low-mid, mid-high and full range (i.e., species living from lowlands to high montane areas). The number of species in each category is shown in Table 1. From hereon we refer to these 6 elevational categories as the elevational state of the species. While this was our main data set, we formulated another data set where the lowlands category was split between lowlands adjacent to mountains and lowlands that are not adjacent to mountains.

We first performed a global analysis in which rates of diversification depend on elevation, resulting in 6 states. We then accounted for the possibility that rates of diversification may differ across latitude and longitude in the following way. We distinguished species occurring in the tropics from species in the temperate (latitudinal analysis), so that latitude and elevation can differentially affect diversification resulting in a model with 12 states (e.g., a species could be a tropical lowland species, or in a temperate mid-high state). We classified species as tropical when most of the latitudinal span of their breeding distribution [48] lies between tropics of Cancer and Capricorn. Finally, we distinguished Old World from New World species (longitudinal analysis, again resulting in 12 possible states (e.g., Old World low-mid state), in which longitude and elevation can differentially affect diversification. We did not perform an analysis where diversification rates simultaneously depend on elevation, latitude and longitude, because the large state space required for such an analysis was computationally unfeasible and numerically unstable given the size of our phylogeny (but see below).

State-dependent diversification analysis and parameterization

We used the SSE framework (State-dependent Speciation and Extinction) which allows determining whether diversification rates are associated with an evolving trait [50]. In this model, the speciation rate (λ_i) or extinction rate (μ_i) of a lineage depends on its trait state *i* (here elevation, or a combination of elevation and latitude (tropical or temperate) or longitude (New World or Old World)). In order to keep the number of estimated parameters as low as possible during the likelihood optimization, we only optimized the speciation (or extinction) rate of the low, mid and high elevation state and used these values to obtain average rates for the states that are a combination of those elevations (e.g., the low and mid elevation rates of speciation are averaged to yield the rate of the low-mid elevation state).

The state of a species is not static, with species switching to a different state at rate q_{ij}, where *i* and *j* represent the state of origin and the state of destination, respectively. This allows us to use trait and branching patterns simultaneously to study macroevolutionary dynamics. In other words, when lineages living in different elevation states experience different speciation/extinction regimes, the shift from one elevational state to another will have an effect on diversification rates. Statistical support for elevation affecting diversification rates is found when the likelihood of a model where speciation (or extinction; see below) differs across elevation states (Elevation-Dependent model, ED) is higher — after correcting for differences in numbers of parameters — than a model where rates depend on an unknown (hidden or concealed) trait (Concealed Trait-Dependent, CTD) and a model with constant rates (CR) [51,52]. The comparison in terms of likelihood between ED and CTD models is important to prevent spurious conclusions regarding the association between heterogeneity in diversification rates across lineages and the evolution of the trait. We used the R package secsse (Several Examined and Concealed States-Dependent Speciation and Extinction; [52]) which computes and optimizes the likelihood of the model with 2 or more states.

We assume that species transition between elevation states via the expansion into an adjacent elevation band (i.e., from low to low-mid or from high to mid-high) or from contraction at the edge of the range (i.e. full range to low-mid or mid-high). In other words, we do not allow disjunct elevational ranges as these are rarely observed [7]. We considered two alternative scenarios for how rates of transitions between states may vary. In both cases we estimate two transition rates. First, under an Uphill-Downhill model, uphill transitions have a different rate than downhill transitions. Note that under the Uphill-Downhill scenario, changing from, for example, the low-mid elevation state to the low elevation state means going downhill. Second, under an expansion-contraction model, all expansion rates (i.e., change from one single elevation band to two, or from two to three) are equal but different from contraction rates (i.e., a change from two bands to a single band, or from three to two bands) which are also equal. We implemented the expansion-contraction model because it allows us to test a scenario where the rate at which species colonize or become extinct at a particular elevation can differ, but where these rates are independent of elevational direction. In other words, in contrast to the Uphill-Downhill model, colonizing (or becoming extinct at) a lower or higher elevation band is equally likely.

As recommended by [29], for the concealed trait we assumed an identical model structure, in terms of the number of states and possible transitions between these. We implemented two versions of the CTD model: one where the transition rates between concealed states are the same as those between elevation states, and one where we relax this assumption and allow the transition rates of the concealed trait to be different from the transition rates between elevational bands. Because differences in diversification rates across elevations could be due to either differential speciation or extinction, we ran all the mentioned model combinations with two different assumptions: in speciation-dependent diversification, speciation varied across states while extinction remained constant. For extinction-dependent diversification, extinction was free to vary across states whereas speciation was kept constant.

In the analysis where we added the state L- that accounts for those lowland species which have limited access to mountain ranges, only Lowland species could expand their distribution uphill. Lineages in L^{-} need first to colonize lowlands close to mountains (L) to then move to higher elevation. In this model, we allow the rates of moving across elevations (or contracting/expanding) to be different from shifting from L^{-} to L (and the reverse) as they are different processes. Uphill-Downhill and Expansion-Contraction model structures are the same as in the global analysis. We ran two versions of this model, one where the rates from L^{-} to L are different as from L to L^{-} and another version where these rates are the same. The results (AICc comparison; **Supplementary Table 4**) point to the former model being preferred. The estimated rate to shift from L^{-} to L is 0.2865 and from L to L^{-} is 0.0106.

For the longitudinal and latitudinal analyses, in addition to allowing different rates of diversification across elevational bands, we also allow the overall rate of diversification to differ between regions (i.e. tropical vs. temperate regions, Old World vs. New World). We did so by multiplying the rates in one region by a constant factor to give rates in the other region and this factor was optimized. To avoid models with many parameters we did not consider the more complex scenario where the elevation-dependence in rates of diversification varies between regions. We assumed that the transition of species between regions (region exchange) happens to and from the same elevational band (low, mid and high only). While we assume that the transition rates *between* regions is the same for all elevational bands, these rates are different from the rates of transition between elevational bands *within* regions.

To prevent finding only local optima during the likelihood optimization, we used five different initial parameter sets. The first set of parameters were the estimates of speciation and extinction from a birth-death model fit to the branching times and with transition rates assumed to be a fifth of speciation rate. For the second set, we doubled the speciation rates of the first set, and halved the transition rates. In the third, we halved the speciation rates of the first set and doubled the transition rates. Similarly, the fourth had doubled extinction rates and halved transition rates, and the fifth had halved extinction rates and doubled transition rates compared to the first set. The highest likelihood of the five starting points was taken as the global optimum and used to compare across models. We used AIC weights – thus penalizing the number of free parameters – to select the best models per analysis.

Our global, latitudinal and longitudinal analyses differ in their assumptions on what factors diversification rates (elevation only, elevation + latitude, elevation + longitude). Using only the data necessary to study these dependencies would prevent model comparison, because the data sets would differ. We had six states in the global analysis (as there are six elevational bands) whereas the longitudinal analysis has 12 states (six bands in combination with tropical and temperate regions) which are different from the 12 states in latitudinal analysis (six bands in combination with New and Old worlds). Therefore, we made the AIC values comparable by adding an extra likelihood term to the likelihood computed by secsse that covers the transitions not covered in secsse, using the function fitDiscrete from the R package geiger [53]. That is, for the longitudinal analysis we added the (maximum) loglikelihood of a simple model of transitions in latitude which uses the phylogenetic tree. In this way, the total likelihood of the longitudinal analysis incorporates the likelihood of a model with transitions across elevations + longitude (computed by secsse) + a model of transitions between latitude (computed by geiger). Note that only the component calculated using secsse handles diversification rates and state transitions simultaneously. Similarly, for the latitudinal analysis we added the (maximum) loglikelihood of a model of transitions in longitude given the phylogenetic tree, and for the global analysis we added the (maximum) loglikelihood of a model of transitions in both longitude and latitude – which in fact is the sum of the two previous loglikelihoods.

Finally, to provide a more direct comparison with previous studies, we also examined the association between elevation and tip diversification rate (tip-DR) using ANOVA and phylogenetic generalized linear model (PGLS) fitted in the R package 'caper'. For our predictor variable we assigned species as either 'highland' (High, Mid-High) or 'lowland' (Low, Low-Mid) and excluded species limited to mid-elevations (Mid) or spanning the entire gradient (Full-Range), resulting in n = 5,186 species. We calculated tip-DR using the 'evol_distinct' function of the 'phyloregion' R package [54].

Data availability

No datasets were generated during the current study. Data analyzed was collected from del Hoyo et al (2016): Handbook of the Birds of the World Alive and from Jetz et al (2012): The global diversity of birds in space and time. Nature 491:444–448.

The necessary files to replicate our study are available at Figshare: 10.6084/m9.figshare.14750652.

Code availability

We used R packages for analyzing data. They are all available at CRAN: caper, phyloregion, DDD and secsse. R code we used to setup models, import, and analyze the output is available (Figshare: 10.6084/m9.figshare.14750652)

TABLES

Supplementary Table 1. Elevational distribution of passerine species richness. We defined three elevational bands: lowlands (from sea level up to 1500 meter above sea level), mid-elevations (1500-3000 m), and highlands (> 3000 m). In temperate regions: lowlands (from 0 to 1000 m), mid-elevations (1000 - 2000 m), and highlands (> 2000 m). Species could also occur in more than one elevational band which adds three more categories: low-mid, mid-high and full range (i.e., species living from lowlands to highlands).

Elevation	Total	Temperate	Tropical	Old World	New World
High	79	27	52	35	44
Mid-High	406	90	316	179	227
Mid	126	13	113	63	63
Low-Mid	2140	314	1826	1367	773
Low	2561	306	2255	1392	1169
Full-range	394	133	261	240	154
Total	5706	883	4823	3276	2430

Supplementary Table 2. Summary of linear models of tip-DR as function of elevation, latitude and their interaction. In models with shared ancestry, species are no longer statistically independent observations in the calculation (i.e., Phylogenetic Generalized Least Squares), in contrast to models where the evolutionary history of species is ignored.

Model	Shared ancestry	F-statistic	Overall probability
Elevation + Latitud + Interaction	no	16.11	p < 0.001
Elevation + Latitud + Interaction	yes	0.8149	p = 0.485
Elevation + Latitud	no	18.6	p < 0.001
Elevation + Latitud	yes	0.7144	p = 0.485
Elevation	no	17.15	p < 0.001
Elevation	yes	1.413	p = 0.234
Latitud	no	16.53	p < 0.001
Latitud	yes	0.019	p = 0.887

Supplementary Table 3. Models of passerine diversification depending on elevation while accounting for potential latitudinal and longitudinal differences (i.e. temperate - tropical and temperate - tropical regions). Speciation or extinction can depend on the elevational range (Elevation-Dependent; ED), or on an unknown trait (Concealed Trait-Dependent; CTD). A model with Constant Rates (CR) across lineages is also included. Models assume explicit constraints (Uphill-Downhill and Expansion-Contraction) on how lineages disperse across elevations over evolutionary time. The fourth column shows whether the examined and concealed traits are assumed to transit at the same rates. When latitudinal analysis is indicated in the fifth column, latitudinal state was incorporated in the secsse analyses (Partial Loglikelihood) whereas longitude was analyzed separately under a simple model of trait evolution and added to obtain the Total Loglikelihood. Likewise, when Longitudinal analysis is indicated, latitude was analyzed separately (see Methods). When Global is indicated, a model of trait evolution that considers the transitions across Latitude and Longitude were analyzed separately. For each model, the number of free parameters *k* is indicated, AIC weights and ΔAIC values are computed using Total Loglikelihoods and used to compare models. Best performing latitudinal, longitudinal and global models are highlighted in gray.

Trait-dependence	Elevation transition mode	Variability across state	Qexamined = Qconcealed?	Type of analysis	Partial Loglikelihood	Total Loglikelihood	*k*	AICw	Δ AIC
CTD	Uphill-Downhill	Speciation	No	Latitudinal	-26730.47	-26785.54	12	~ 0.99	0

CTD	Uphill-Downhill	Speciation	Yes	Latitudinal	-26856.93	-26912.00	9	< 0.0001	247
ED	Uphill-Downhill	Speciation	Yes	Latitudinal	-27069.99	-27125.06	9	< 0.0001	673
ED	Uphill-Downhill	Speciation	No	Latitudinal	-27070.06	-27125.13	12	< 0.0001	679
CR	Uphill-Downhill	Speciation	Yes	Latitudinal	-27287.98	-27343.05	6	< 0.0001	1103
ED	Uphill-Downhill	Extinction	Yes	Latitudinal	-27287.94	-27343.01	9	< 0.0001	1109
CR	Uphill-Downhill	Speciation	No	Latitudinal	-27307.17	-27362.24	9	< 0.0001	1147
CTD	Uphill-Downhill	Extinction	No	Latitudinal	-27310.58	-27365.65	12	< 0.0001	1160
ED	Uphill-Downhill	Extinction	No	Latitudinal	-27329.65	-27384.72	12	< 0.0001	1198
CTD	Uphill-Downhill	Speciation	No	Global	-24927.06	-27418.86	10	< 0.0001	1263
CTD	Uphill-Downhill	Extinction	Yes	Latitudinal	-27409.29	-27464.36	9	< 0.0001	1352
CTD	Uphill-Downhill	Speciation	Yes	Global	-24980.61	-27472.41	8	< 0.0001	1366
CTD	Expansion-Contraction	Speciation	No	Latitudinal	-27735.41	-27790.48	12	< 0.0001	2010
CTD	Expansion-Contraction	Speciation	No	Global	-25322.63	-27814.43	10	< 0.0001	2054
CTD	Expansion-Contraction	Speciation	Yes	Global	-25335.06	-27826.86	8	< 0.0001	2075
ED	Uphill-Downhill	Speciation	Yes	Global	-25336.69	-27828.49	8	< 0.0001	2078
ED	Uphill-Downhill	Speciation	No	Global	-25336.94	-27828.74	10	< 0.0001	2082
CTD	Uphill-Downhill	Speciation	No	Longitudinal	-25491.37	-27928.10	12	< 0.0001	2285

CTD	Expansion-Contraction	Speciation	Yes	Latitudinal	-27877.70	-27932.77	9	< 0.0001	2288
CR	Uphill-Downhill	Speciation	Yes	Global	-25472.91	-27964.72	6	< 0.0001	2346
ED	Uphill-Downhill	Extinction	Yes	Global	-25472.88	-27964.68	8	< 0.0001	2350
CR	Uphill-Downhill	Speciation	No	Global	-25472.91	-27964.72	8	< 0.0001	2350
CTD	Uphill-Downhill	Extinction	Yes	Global	-25472.92	-27964.72	8	< 0.0001	2350
ED	Uphill-Downhill	Extinction	No	Global	-25472.88	-27964.68	10	< 0.0001	2354
CTD	Uphill-Downhill	Extinction	No	Global	-25476.31	-27968.11	10	< 0.0001	2361
CTD	Uphill-Downhill	Speciation	Yes	Longitudinal	-25548.50	-27985.23	9	< 0.0001	2393
ED	Expansion-Contraction	Speciation	Yes	Latitudinal	-28191.26	-28246.33	9	< 0.0001	2916
ED	Expansion-Contraction	Speciation	Yes	Global	-25756.98	-28248.78	8	< 0.0001	2918
ED	Expansion-Contraction	Speciation	No	Global	-25766.41	-28258.21	10	< 0.0001	2941
ED	Expansion-Contraction	Speciation	No	Latitudinal	-28218.90	-28273.97	12	< 0.0001	2977
ED	Uphill-Downhill	Speciation	Yes	Longitudinal	-25848.43	-28285.16	9	< 0.0001	2993
ED	Uphill-Downhill	Speciation	No	Longitudinal	-25870.24	-28306.97	12	< 0.0001	3043
ED	Expansion-Contraction	Extinction	No	Global	-25830.22	-28322.02	10	< 0.0001	3069
CR	Expansion-Contraction	Speciation	Yes	Global	-25841.22	-28333.02	6	< 0.0001	3083
ED	Expansion-Contraction	Extinction	Yes	Global	-25840.72	-28332.52	8	< 0.0001	3086

CR	Expansion-Contraction	Speciation	No	Global	-25841.22	-28333.02	8	< 0.0001	3087
CTD	Expansion-Contraction	Extinction	Yes	Global	-25841.23	-28333.03	8	< 0.0001	3087
CTD	Expansion-Contraction	Extinction	No	Global	-25841.24	-28333.04	10	< 0.0001	3091
CTD	Expansion-Contraction	Speciation	Yes	Longitudinal	-25914.45	-28351.18	9	< 0.0001	3125
CTD	Expansion-Contraction	Speciation	No	Longitudinal	-25923.45	-28360.18	12	< 0.0001	3149
ED	Expansion-Contraction	Extinction	Yes	Latitudinal	-28309.92	-28364.99	9	< 0.0001	3153
CR	Expansion-Contraction	Speciation	Yes	Latitudinal	-28424.00	-28479.07	6	< 0.0001	3375
ED	Expansion-Contraction	Extinction	No	Latitudinal	-28420.98	-28476.05	12	< 0.0001	3381
CR	Expansion-Contraction	Speciation	No	Latitudinal	-28424.00	-28479.07	9	< 0.0001	3381
CTD	Expansion-Contraction	Extinction	Yes	Latitudinal	-28424.01	-28479.08	9	< 0.0001	3381
CR	Uphill-Downhill	Speciation	Yes	Longitudinal	-26047.86	-28484.59	6	< 0.0001	3386
CTD	Expansion-Contraction	Extinction	No	Latitudinal	-28424.00	-28479.07	12	< 0.0001	3387
CR	Uphill-Downhill	Speciation	No	Longitudinal	-26047.87	-28484.60	9	< 0.0001	3392
ED	Uphill-Downhill	Extinction	No	Longitudinal	-26047.69	-28484.42	12	< 0.0001	3398
CTD	Uphill-Downhill	Extinction	No	Longitudinal	-26047.91	-28484.64	12	< 0.0001	3398
ED	Uphill-Downhill	Extinction	Yes	Longitudinal	-26075.04	-28511.77	9	< 0.0001	3446
CTD	Uphill-Downhill	Extinction	Yes	Longitudinal	-26113.74	-28550.47	9	< 0.0001	3524

ED	Expansion-Contraction	Speciation	Yes		Longitudinal	-26403.33	-28840.06	9	< 0.0001	4103
ED	Expansion-Contraction	Speciation	No		Longitudinal	-26409.87	-28846.60	12	< 0.0001	4122
ED	Expansion-Contraction	Extinction	Yes		Longitudinal	-26515.80	-28952.53	9	< 0.0001	4328
CR	Expansion-Contraction	Speciation	Yes		Longitudinal	-26574.03	-29010.76	6	< 0.0001	4438
CR	Expansion-Contraction	Speciation	No		Longitudinal	-26574.03	-29010.76	9	< 0.0001	4444
CTD	Expansion-Contraction	Extinction	Yes		Longitudinal	-26574.03	-29010.76	9	< 0.0001	4444
ED	Expansion-Contraction	Extinction	No		Longitudinal	-26572.24	-29008.97	12	< 0.0001	4447
CTD	Expansion-Contraction	Extinction	No		Longitudinal	-26574.03	-29010.76	12	< 0.0001	4450

Supplementary Table 4. Models of passerine diversification depending on elevation while considering the spatial configuration of lowlands. Speciation or extinction can depend on the elevational range (Elevation-Dependent; ED), or on an unknown trait (Concealed Trait-Dependent; CTD). A model with Constant Rates (CR) across lineages is also included. Models assume explicit constraints (Uphill-Downhill and Expansion-Contraction) on how lineages disperse across elevations over evolutionary time. Different from the analysis shown in Extended Data Table 3, the models we compare in this table include an additional state (L-) which represents those lineages that cannot colonize higher elevations (i.e., island species or species far from mountain ranges). In this model, only Lowland species (see Figure 2) can expand their distribution uphill and lineages in L- need first to colonize lowlands to then move to higher elevation. In this model, the rates of moving across elevations (or contracting/expanding) are different from shifting from L- to Lowlands (and the reverse) as they are different processes. The fourth column shows whether the rates from L- to Lowlands are different than from Lowlands to L-. For each model, the number of free parameters *k* is indicated and AIC weights are computed to compare models.

Trait-dependence	Elevation transition mode	Variability across state	Asymmetric Foothill Dispersal	Loglikelihoods	k	AICw
CTD	Uphill-Downhill	Speciation	Yes	-25313.8	8	~ 0.99
CTD	Uphill-Downhill	Speciation	No	-25464.8	7	< 0.0001
CTD	Expansion-Contraction	Speciation	Yes	-25813	8	< 0.0001
ETD	Uphill-Downhill	Speciation	Yes	-25856.5	8	< 0.0001
CTD	Uphill-Downhill	Extinction	Yes	-25938.3	8	< 0.0001

CR	Uphill-Downhill	Speciation	Yes	-26005	6	< 0.0001
ETD	Uphill-Downhill	Extinction	Yes	-26004.9	8	< 0.0001
CTD	Expansion-Contraction	Speciation	No	-26020.4	7	< 0.0001
ETD	Uphill-Downhill	Speciation	No	-26026.3	7	< 0.0001
CR	Expansion-Contraction	Speciation	No	-26553.6	5	< 0.0001
CR	Expansion-Contraction	Speciation	Yes	-26349.8	6	< 0.0001
CR	Uphill-Downhill	Speciation	No	-26162.5	5	< 0.0001
CTD	Expansion-Contraction	Extinction	No	-26437.6	7	< 0.0001
CTD	Expansion-Contraction	Extinction	Yes	-26257.6	8	< 0.0001
CTD	Uphill-Downhill	Extinction	No	-26074.6	7	< 0.0001
ETD	Expansion-Contraction	Speciation	No	-26458.7	7	< 0.0001
ETD	Expansion-Contraction	Speciation	Yes	-26263.6	8	< 0.0001
ETD	Expansion-Contraction	Extinction	No	-26285.5	7	< 0.0001
ETD	Expansion-Contraction	Extinction	Yes	-26066.3	8	< 0.0001
ETD	Uphill-Downhill	Extinction	No	-26159.3	7	< 0.0001